

and cytogenetic studies are needed to determine the status (probably intraspecific) of the variants in our area."

A close relative of *Piriqueta caroliniana* is *P. cistoides*, a widely distributed rather weedy plant that occurs in the Greater Antilles and the Lesser Antilles, and also ranges from Mexico through Central America into Brazil (Urban, 1883). Although described as an annual, some plants of this species will continue to flower for at least three years in cultivation.

*Piriqueta cistoides* is variable throughout its range. Urban (1883) recognized eight varieties in this species. *Piriqueta cistoides* var. *cistoides* is the most widely distributed and occurs almost throughout the range of the species; in pubescence characters it resembles *P. caroliniana* var. *caroliniana*. Four of the varieties are restricted to mainland South America, one is endemic to Jamaica, and two occur in both the West Indies and on the South American continent. In general, however, subsequent authors (including Urban, 1920) have not recognized infraspecific taxa in *P. cistoides* (e.g., Boldingh, 1913; Fawcett & Rendle, 1926; Standley, 1928; Stahl, 1936; and Alain, 1957).

*Piriqueta caroliniana* and *P. cistoides* are diploid with  $n = 7$  (TABLE 1; Lewis et al., 1962). The most consistent morphological differences between them are floral ones. *Piriqueta caroliniana* has large, distylous, and strongly self-incompatible flowers; *P. cistoides* has small, homostylous, and largely autogamous flowers.

#### HYBRIDIZATION PROGRAM

A program of artificial inter- and intraspecific hybridizations was carried out with *Piriqueta caroliniana* and *P. cistoides*. Plants of *P. caroliniana* used in this program were referable to each of the morphological variants recognized by Small (1933; TABLE 1). Three of the collections of *P. cistoides* were referable to var. *cistoides*; the Trinidad plants were closest to var. *latifolia* Urb. (TABLE 1). Seeds from South American and Meso-American populations of these species have not been available, and, as a result, this study has been limited to representatives from the southeastern United States and the West Indies.

Artificial hybridizations were carried out in insect-proof cages in the greenhouse. The large, self-incompatible flowers of *Piriqueta caroliniana* were not emasculated prior to hybridization, but the anthers of the small, autogamous flowers of *P. cistoides* were removed before anthesis to prevent self-pollination. Intraspecific interpopulation hybridizations are easily accomplished in *P. caroliniana* and result in a full seed-set. In contrast, the seed-set following such hybridizations within *P. cistoides* is reduced, possibly because of damage to the flowers as a result of removal of the anthers. Interspecific hybridizations were possible only when *P. cistoides* served as the seed parent, indicating the presence of a unilateral incompatibility system. When the hybrids flowered, pollen samples from them



TABLE 1. Origin and chromosome numbers of collections of *Piriqueta* used in crossing program

	TAXON	DESIGNATION	CHROMOSOME NUMBER	ORIGIN
(P. cistoides var.)	<i>cistoides</i>	Dominica	$n = 7$	Dominica, West Indies, <i>W. R. Ernst 2141</i> .
	<i>cistoides</i>	Jamaica		Kingston, Jamaica, <i>M. Crosby, H. Hespenheide, &amp; W. Anderson 1264</i> .
	<i>cistoides</i>	Puerto Rico		Near Mayaguez, Puerto Rico, <i>F. W. Martin s.n.</i>
	<i>latifolia</i>	Trinidad	$n = 7$	St. Augustine, Trinidad, <i>J. W. Purseglove s.n.</i>
(P. caroliniana var.)	<i>glabrescens</i>	1519		Florida. Collier County: east of Monroe Station, <i>J. D. Perry 1519</i> .
	<i>caroliniana</i>	6454 <sup>1</sup>	$n = 7$	South Carolina. Orangeburg County: west of Santee.
	<i>tomentosa</i>	6743		Florida. Hillsborough County: Tampa.
	<i>glabrescens</i>	6746	$n = 7$	Florida. Collier County: east of Naples.
	<i>tomentosa-viridis-glabrescens</i> <sup>2</sup>	6750	$n = 7$	Florida. Dade County: southwest of Homestead.
	<i>caroliniana</i>	6752	$2n = 14$	Florida. Dade County: west of Perrine.
	<i>tomentosa-caroliniana</i> <sup>2</sup>	6754	$n = 7$	Florida. Dade County: Suniland.
	<i>viridis</i>	6755	$n = 7$	Florida. Glades County: southeast of Palm-dale.
	<i>caroliniana</i>	6758	$n = 7$	Florida. Highlands County: south of DeSoto City.
	<i>caroliniana</i>	6762		South Carolina. Jasper County: near Har-dee-ville.

<sup>1</sup> Collection numbers are those of the author unless otherwise noted.

<sup>2</sup> Population contains plants referable to each taxon or intermediate between the taxa.



were mounted in aniline blue-lactophenol and scored for viability on the basis of their staining reaction (TABLE 2).

## RESULTS

Fifteen hybrid progenies of *Piriqueta caroliniana* representing 14 inter-population combinations were obtained (TABLES 1, 2). The average

TABLE 2. Results of artificial hybridizations of *Piriqueta caroliniana* and *P. cistoides*

CROSS	AVERAGE POLLEN VIABILITY	(RANGE OF POLLEN VIABILITIES; NUMBER OF PLANTS IN PROGENY)
[Intraspecific hybridizations: <i>P. caroliniana</i> ]		
6454 × 6755 <sup>1</sup>	88	(64-99; 5)
Reciprocal	76	(59-99; 7)
6454 × 6758	89	(72-100; 5)
6743 × 6746	90	(75-98; 8)
6743 × 6754	94	(84-97; 6)
6746 × 6750	93	(82-100; 12)
6746 × 6754	92	(76-99; 4)
6752 × 6746	70	(43-99; 4)
6754 × 6454	90	(79-97; 8)
6754 × 6750	92	(80-100; 15)
6754 × 6755	94	(80-98; 6)
6755 × 6743	86	(75, 98; 2)
6755 × 6746	95	(86-100; 5)
6762 × 6743	96	(93-100; 6)
6762 × 6755	97	(85-100; 11)
[Intraspecific hybridizations: <i>P. cistoides</i> ]		
Dominica × Jamaica	43	(39-46; 4)
Reciprocal	48	(35-60; 6)
Dominica × Puerto Rico	46	( - ; 1)
Reciprocal	57	(40-69; 6)
Dominica × Trinidad	34	(22, 46; 2)
Reciprocal	19	(17, 21; 2)
Jamaica × Puerto Rico	96	(95, 98; 2)
Reciprocal	95	(92-97; 3)
Trinidad × Jamaica	61	(50-81; 7)
F <sub>2</sub>	37	(1-63; 6)
Trinidad × Puerto Rico	72	(68-78; 6)
(Interspecific hybridizations)		
Trinidad × 1519	74	(74, 75; 2)
F <sub>2</sub>	48	(0-80; 11)
Trinidad × 6454	68	(9-90; 22)
F <sub>2</sub>	46	(2-81; 8)
Trinidad × 6746	75	(60-92; 7)
Trinidad × 6755	75	(47-86; 9)
F <sub>2</sub>	53	(32, 74; 2)

<sup>1</sup> See TABLE 1 for origin and further identification of these populations. In the left-hand column the seed parent is listed first.



pollen viabilities of 13 of these progenies were above 85 percent. Two hybridizations produced progenies with average pollen viabilities below 85 percent. However, the reciprocal of one of these crosses produced progeny with a high average pollen viability. The other of the progenies involved parental taxa (vars. *caroliniana* and *glabrescens*) which produced fertile progeny when individuals from other populations were hybridized. These results indicate there are no consistent internal barriers to hybridization among the morphological variants of *P. caroliniana*, nor is sterility prevalent in the hybrid progeny.

Examination of the morphology of the  $F_1$  hybrids in *Piriqueta caroliniana* indicates a tendency for pubescence characteristics of the more pubescent parent to be expressed in the progeny. For example, hybrids between parents with the *caroliniana* (hirsute and tomentose herbage) and *viridis* (glabrous) phenotypes resemble the *caroliniana* parent; those between *glabrescens* (tomentose pedicel and calyx only) and *viridis* phenotypes resemble the *glabrescens* parent. Those between *tomentosa* (tomentose herbage) or *caroliniana* and *glabrescens* resemble either of the first two parents. Thus, the hybrids are not intermediate between the parents in the pubescence characters which have provided the chief morphological bases for making a taxonomic distinction between them.

Ten hybrid progenies of *Piriqueta cistoides* representing six combinations of parents originating on different West Indian islands were grown (TABLE 2). Reciprocal hybrid progenies were grown for four of these hybrid combinations. With one exception, the hybrid progenies of *P. cistoides* exhibited a reduced pollen viability. The average pollen viability of the single  $F_2$  generation was lower than that of the  $F_1$ . The pattern of low interpopulation pollen fertility in *P. cistoides* provides a sharp contrast with the pattern obtained in *P. caroliniana*.

Four progenies were obtained as a result of artificial hybridizations between plants of the Trinidad collection of *P. cistoides* and *P. caroliniana*; hybridizations using other collections of *P. cistoides* failed to produce seed. The average pollen viabilities of these interspecific hybrid progenies ranged from 68 per cent to 75 per cent (TABLE 2). A reduction in average pollen viability occurred in the three  $F_2$  generations that were grown.

## DISCUSSION

There are no consistent sterility barriers separating the morphologically distinctive variants of *Piriqueta caroliniana* in the southeastern United States that have been accorded taxonomic status by some authors. This indicates that these distinctive variants of *P. caroliniana* are very closely related genetically. The ease of making artificial hybrids among them, and the generally high fertility of the resultant  $F_1$  hybrids and of subsequent generations, may explain in part the occurrence of natural populations which share characters of two or more of the segregate taxa, since in many areas of Florida populations of two or more of these taxa occur in close proximity. Nevertheless, the majority of herbarium specimens I



have examined at FLAS, FSU, and USF are referable to these taxa and show no obvious indication of hybridization. Some years ago Dr. J. D. Perry mapped the distribution of these variants in Florida, based on his examination of herbarium specimens at DUKE, GA, NCU, NSC, and US. Examination of his unpublished map indicates that populations of *P. caroliniana* var. *caroliniana* and var. *tomentosa* are considerably more abundant than are those of vars. *glabrescens* and *viridis*, and, furthermore, that the latter two taxa are confined to the southern half of peninsular Florida. It seems possible that field studies may reveal the existence of differences in ecological tolerances of these four taxa and that the differences may provide the basis for their continued genetic and morphological integrity over much of their ranges.

The low interpopulation crossability and the associated hybrid sterility in *Piriqueta cistoides* are unexpected in view of the contrast these results provide with the behavior of the closely related *P. caroliniana*. The degree of morphological differentiation among the plants of *P. cistoides* used in the crossing program was considerably less than that in material of *P. caroliniana*. Nevertheless, in *P. cistoides* this low degree of differentiation is in general associated with a genetic variability that results in a reduced pollen fertility of intraspecific hybrids. The high genetic individuality of each population of *P. cistoides* may be related to the autogamous breeding system and weedy habit of the species. It is probable that many of its populations are built up from one or a few initial colonizers of disturbed land. These populations are consequently rather uniform genetically. Homozygosity for random genetic changes or alterations in chromosome structure can become rapidly established in autogamous annuals, particularly under conditions where there are fluctuations in population size. In an outcrossing non-weedy perennial of stable habitats such as *P. caroliniana*, the establishment of homozygosity for such random cytogenetic changes would be a slower process, even when generation time is taken into consideration. In addition, the genetic individuality of the populations of *P. cistoides* undoubtedly is strongly reinforced by the spatial isolation of the populations on West Indian islands. This speculation suggests, therefore, that the observed differences in the fertility of interpopulation hybrids of *P. cistoides* compared with those of *P. caroliniana* is a consequence of the differences in the breeding systems, duration, population structure, and distribution patterns of these two morphologically similar species.

The close relationship between *Piriqueta cistoides* and *P. caroliniana* is indicated by their strong morphological similarity and by the moderately high fertility of their interspecific hybrids. The floral differences which separate *P. cistoides* and *P. caroliniana* are those which are associated with their different breeding systems. The showy, heterostylous flowers of *Piriqueta caroliniana* are outcrossed by halictid bees (Ornduff & Perry, 1964). In contrast, the flowers of *P. cistoides* are homostylous and are usually self-pollinated before anthesis. The smaller perianth and the reduced length of the reproductive structures of the flowers of *P. cistoides*



represent a familiar syndrome of features by which an autogamous species differs from its allogamous relatives (see Ornduff, 1969, p. 128). The floral morphology of *P. cistoides* indicates that this species has been derived from a heterostylous ancestor. The flowers of *P. cistoides* are long-homostylous, that is, they fundamentally combine a long style with the stamen length and pollen size of short-styled flowers (Ornduff, unpublished). Where heterostyly and homostyly occur in closely related taxa, homostyly is considered to be a derivative condition. Evidence from morphology, geographical distribution, and artificial hybridizations suggests that *P. caroliniana* is the probable ancestor of *P. cistoides*. The results of this study have been useful in assessing genetic relationships among populations of these two species and also in explaining some of the differences in their variation patterns. Although these results may be pertinent to the taxonomic decisions that ultimately must be made in this group, the decisions will have a stronger foundation if they include a consideration of careful field, herbarium, and nomenclatural studies.

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## A REVISION OF THE BORAGINACEAE OF WEST PAKISTAN AND KASHMIR \*

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### 15. *Lappula* Gilib. Fl. Lithuan. 25. 1781.

*Echinospermum* Sw. ex Lehm. Asperif. 1: 113. 1818.

TYPE SPECIES: not indicated.

Annuals, rarely biennials or perennials. Leaves alternate. Inflorescence bracteate. Calyx divided to the base, lobes after flowering not at all to slightly enlarged. Corolla blue or white, funnelform to salverform. Fau- cal appendages present. Anthers included. Gynobase narrowly pyramidal. Style short, filiform; stigma capitate. Nutlets 4, attached throughout their length to the gynobase, sometimes apices free on the inner face, appendic- ulate, appendages glochidiate to aculeate.

About 45 species, usually distributed in temperate Europe and Asia, few in Africa, one in America.

### KEY TO THE SPECIES

- a. Nutlets smooth, tuberculate all over their surface; tubercles large, thorn- like, neither prickly nor bearing glochidia at their apices.
  - b. Nutlets pyramidal to ovate-pyramidal in outline, usually longer than broad, tubercles less unequal, basal ones not much enlarged. . . . . 1. *L. spinocarpos*.
  - b. Nutlets broadly pyramidal in outline, usually broader than long, tubercles very unequal, basal ones much enlarged. . . . . 2. *L. ceratophora*.
- a. Nutlets usually rough, appendiculate at the margins, appendages bearing glochidia at their apices, usually tuberculate, on the dorsal and ventral sur- faces, tubercles small, very rarely tuberculate only.
  - c. Nutlets usually not, or only rarely, indistinctly margined with few glo- chidiate appendages; usually indistinctly verruculose, more or less smooth. . . . . 3. *L. sinaica*.
  - c. Nutlets distinctly margined with appendages, appendages glochidiate.
    - d. Flowers and fruits sessile, fruits pyramidal, nutlets triangular, mar- ginal appendages usually dilated at base, bases joined to form a narrow marginal wing. . . . . 4. *L. sessiliflora*.
    - d. Flowers and fruits with short to long pedicels, fruits ovate, nutlets ovate to oblong, marginal appendages not at all to slightly dilated at base, bases not joined to form a marginal wing.
      - e. Nutlets with uniseriate marginal appendages.
        - f. Inflorescence strongly elongated; nutlets small, 2-3 mm. long; marginal appendages always less than 1 mm. long; leaves linear; bracts small. . . . . 5. *L. microcarpa*.

\* Continued from volume 51, p. 402.